

Hypostomus khimaera Tencatt, Zawadzki & Fröhlich, 2014 (Siluriformes, Loricariidae) in the upper rio Paraná basin, Brazil: first record and comments on its occurrence

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Abstract. *Hypostomus khimaera* Tencatt, Zawadzki & Fröhlich, 2014 is a species native to the rio Paraguay basin, but it is recorded here from the upper rio Paraná basin for the first time. Our new record was made in the córrego Mimoso, a tributary of the rio Anhanduí, approximately 180 km from the closest previously reported locality. We are unsure whether the occurrence of this species in the upper rio Paraná basin is a consequence of natural phenomena, such as headwater connection during floods or stream capture, or an artificial introduction. Together with the invasive *H. cochliodon* Kner, 1854, *H. khimaera* is the second species of the *H. cochliodon* group recorded in the upper rio Paraná basin. Here, we provide an updated diagnosis of *H. khimaera* and highlight the differences in opercle exposition as the easiest way to differentiate it from the syntopic and morphologically similar *H. cochliodon*.

Key words. Geographic distribution, *Hypostomus cochliodon* group, rio Anhanduí basin, species distribution, species sharing

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INTRODUCTION

Widely distributed and currently comprising more than 150 valid species, *Hypostomus* Lacépède, 1803 is one of the most species-rich genera of Neotropical freshwater fishes (Silva et al. 2016; Queiroz et al. 2020; Fricke et al. 2024). The *Hypostomus cochliodon* group (*sensu* Armbruster 2003) currently harbors 22 species, which can be distinguished from the remaining congeners by having teeth with mesial cusp ranging from shovel-shaped or spatulate to spoon-shaped (except for young *H. khimaera*, which can present villiform teeth; Tencatt et al. 2014), loss of a notch between the metapterygoid and the hyomandibula, and strongly angled dentaries, with up to about 80° between dentaries (Armbruster 2003, 2004; Tencatt et al. 2014; Oliveira et al. 2020).

In the Paraná–Paraguay system, three species of the *H. cochliodon* group are recognized: *H. cochliodon* Kner, 1854, *H. basilisko* Tencatt, Zawadzki & Fröhlich, 2014, and *H. khimaera* Tencatt, Zawadzki & Fröhlich, 2014; all were described from the upper rio Paraguay basin (Tencatt et al. 2014, 2022). Among these species, only *H. cochliodon* has been recorded in the upper rio Paraná basin, where it has been considered a non-native or allochthonous species (Graça and Pavanelli 2007; Langeani et al. 2007; Froehlich et al. 2017; Ota et al. 2018; Dagosta et al. 2024). *Hypostomus cochliodon* was putatively introduced to the



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upper rio Paraná basin ecoregion through the impoundment of the rio Paraná to form the Itaipu Reservoir (Graça and Pavanelli, 2007; Ota et al. 2018; Dagosta et al. 2024), which flooded the Sete Quedas waterfalls, a former biogeographic barrier between the upper and lower rio Paraná basin (Benedito Cecílio et al. 1997). In this study, we present the first record of *H. khimaera* in the upper rio Paraná basin. This species was originally described from tributaries of the upper rio Paraguay and until now it had not been recorded outside this river basin. We discuss the occurrence of this species in the upper rio Paraná basin and provide diagnostic characters to distinguish it from other *H. cochliodon* group species.

METHODS

One individual of *Hypostomus khimaera* was collected on 3 October 2023 in the córrego Mimoso, near the mouth on rio Anhanduí, tributary of the rio Pardo, upper rio Paraná basin, Ribas do Rio Pardo municipality, Mato Grosso do Sul state, Brazil. The sampling was done as part of an inventory for a new conservation unit in the region of the Pardo and Anhanduí rivers. The specimen was collected in an artisanal trawl measuring 1.5×1 m. It was euthanized by eugenol overdose in accordance with Lucena et al. (2013). After death, the specimen was fixed in a 4% formaldehyde solution, where it was kept for 48 h and then transferred to 70% ethanol. This voucher specimen is deposited in the Coleção Ictiológica de Três Lagoas (CITL). The collection was authorized by the Sistema Nacional de Informação da Biodiversidade of Brazil (SISBio permit 81153/6 – 2023).

Measurements were made with digital calipers having a precision of 0.1 mm. Measurements follow Boeseman (1968), with the modifications adopted by Tencatt et al. (2014). To access previously recorded distributional data on *H. khimaera*, we searched for lots with geographic coordinates in collection databases hosted on the SpeciesLink website (CRIA 2024). The resulting data were plotted in a map using QGIS v. 3.30.2.

RESULTS

Hypostomus khimaera Tencatt, Zawadzki & Fröhlich, 2014

Figures 1, 2, Table 1

New record. BRAZIL – MATO GROSSO DO SUL • upper rio Paraná basin, rio Pardo sub-basin, Ribas do Rio Pardo, córrego Mimoso, tributary of the rio Anhanduí; $21^{\circ}31'48''\text{S}$, $053^{\circ}26'47''\text{W}$; 297 m alt.; 3.X.2023; D.A. Lopes, R.N. de Souza & T.F. Sinani leg.; CITL 1015, 1 spec., alcohol, 75.9 mm SL (Figure 2).

Identification. *Hypostomus khimaera* can be distinguished from congeners, except the species in the *H. cochliodon* group, by the absence of a notch between metapterygoid and hyomandibula and by the strongly angled dentaries, with up to about 80° between dentaries (vs. more obtusely angled dentaries, with clearly more than 80° between dentaries) (Tencatt et al. 2014). It can be distinguished from other species of the *Hypostomus cochliodon* group, except *H. basilisko* and *H. soniae* Hollanda Carvalho & Weber, 2005 by the presence of a dark stripe along the midline on flank (vs. absence of midline stripe). *Hypostomus khimaera* differs from *H. basilisko* and *H. soniae* by the presence of black spots on the body

Figure 1. *Hypostomus khimaera* photographed alive in lateral view. **A.** Specimen from córrego Mimoso, tributary of the rio Anhanduí, rio Pardo basin, upper rio Paraná basin (CITL 1015, 75.9 mm SL). **B.** Specimen from the rio Sepotuba basin, upper rio Paraguay basin, Mato Grosso (uncatalogued, about 250.0 mm SL).



Figure 2. Distribution of *Hypostomus khimaera*. Black circles = previously known records in the SpeciesLink database (CRIA 2024); yellow star = new record in upper rio Paraná basin.

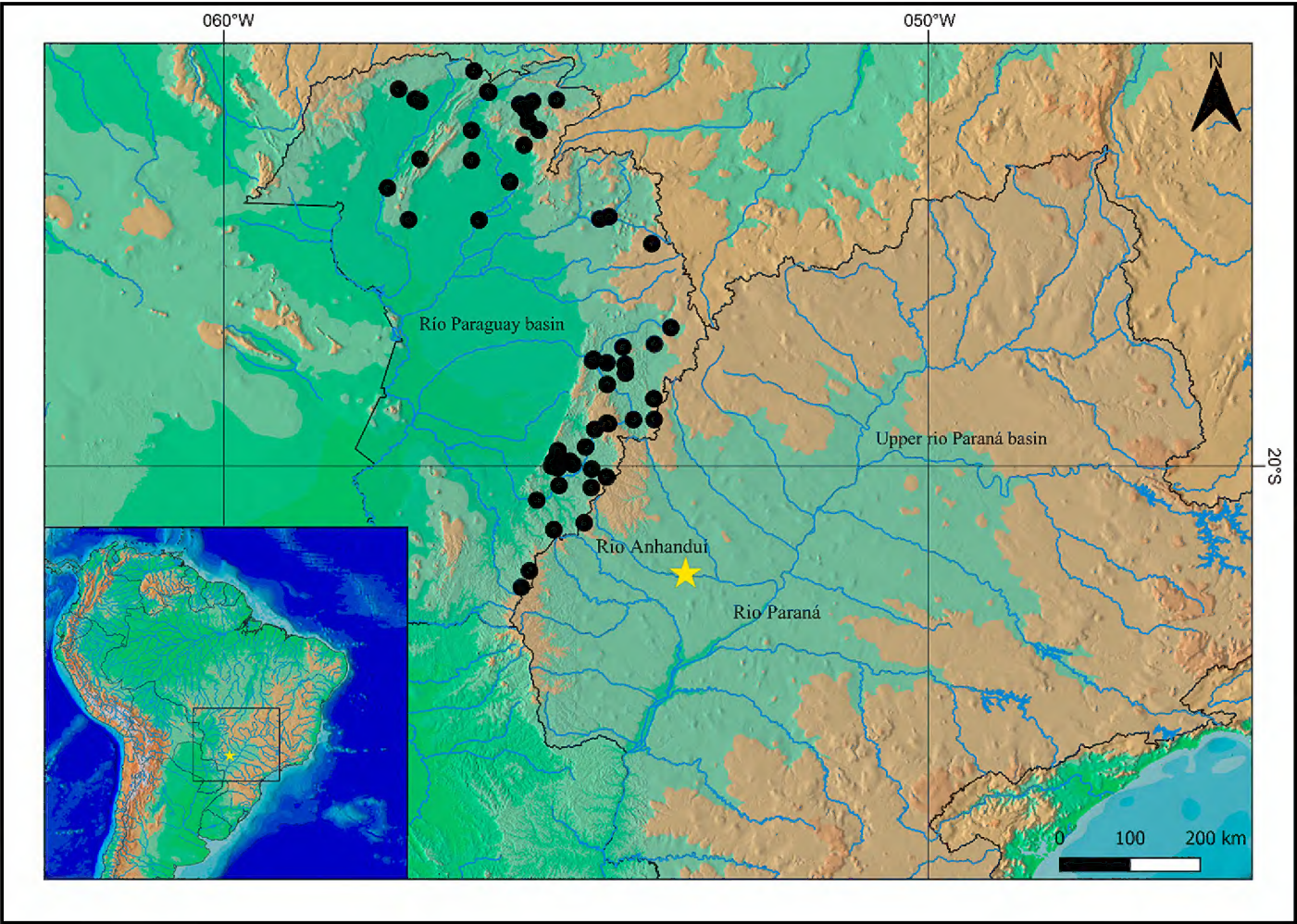


Table 1. Morphometric data of *Hypostomus khimaera* collected in córrego Mimoso, upper rio Paraná basin, Brazil (CITL 1015).

Measurements	CITL 1015
Standard length (mm)	75.9
Percents of standard length	
Predorsal length	43.7
Head length	35.8
Interdorsal distance	15.1
Thoracic width	21.8
Abdominal width	20.4
Caudal peduncle length	32.8
Caudal peduncle depth	11.0
Dorsal-fin spine length	31.2
Dorsal-fin base length	25.4
Pectoral-fin spine length	28.5
Pelvic-fin spine length	26.6
Dorsal caudal-fin ray length	29.0
Ventral caudal fin-ray length	42.0
Adipose-fin spine length	7.2
Cleithral width	33.1
Percents of head length	
Head depth	68.5
Snout length	67.2
Interorbital width	47.6
Orbital diameter	16.5
Lower lip width	43.7
Lower lip length	13.7
Mandibular ramus length	15.6
Maxillary barbel length	12.9

and/or fins and moderately developed keels and odontodes (vs. black spots absent from body and fin and strongly developed keels and numerous well-developed odontodes). *Hypostomus khimaera* is additionally distinguished from *H. cochliodon* by the greater number of teeth (12–27 vs. 7–9), by having an externalized opercle with the exposed region easily visible (vs. almost entirely internalized opercle with exposed region not easily visible), weakly developed papillae on both upper and lower jaws, not forming series (vs. papillae well developed, forming one series on the inner face of both upper and lower jaw), moderately developed keels, with moderately developed odontodes (vs. weakly developed keels and odontodes) (Tencatt et al. 2014; Figures 3, 4). The specimen collected in the córrego Mimoso, upper rio Paraná basin, presents the combination of characters described for *H. khimaera*: acutely angled dentary (less than 80°), a dark stripe along flank midline, black spots on body and fins, 14 teeth on premaxilla, and an externalized opercle with exposed region easily visible.

DISCUSSION

Hypostomus khimaera was described by Tencatt et al. (2014) from the córrego Salobo (the type locality), a tributary of the rio Paraguay in Mato Grosso, and was considered to be endemic to the rio Paraguay basin. It occurs in a variety of habitats, such as rapids and marginal habitats with sandy substrate, and is most associated with small streams, although occasionally found in the main channel of larger rivers (Tencatt et al. 2022). Its previously known distribution extends between the upper rio Paraguay and rio Cuiabá basins to the north and the rio Aquidauana, to the south. However, it is mostly confined to the upper portions of the rio Paraguay basin, in the plateau area surrounding the Pantanal (Tencatt et al. 2014: 594, fig. 9), which is demonstrated by the 85 lots of *H. khimaera* in the SpeciesLink database (CRIA 2024) (Figure 2). In the

Figure 3. Living specimens in lateral view, evidencing the differences on opercula morphology. **A.** *Hypostomus khimaera* recorded in the upper rio Paraná basin (CITL 1015, 75.9 mm SL). **B.** *Hypostomus khimaera* from upper rio Paraguay basin (uncatalogued, about 250.0 mm SL) **C.** *Hypostomus cochliodon* from upper rio Paraguay basin (uncatalogued, about 350.0 mm SL).

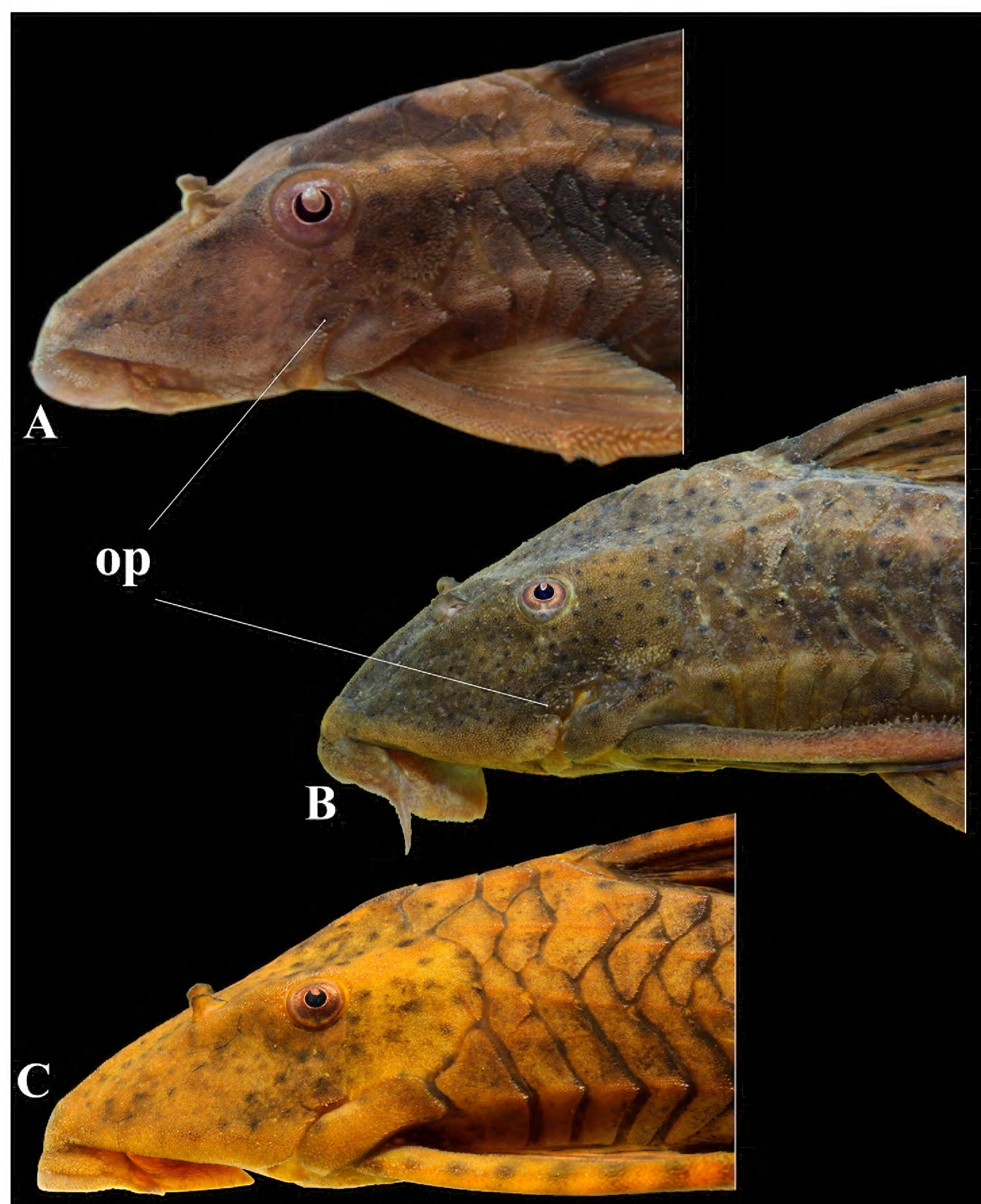
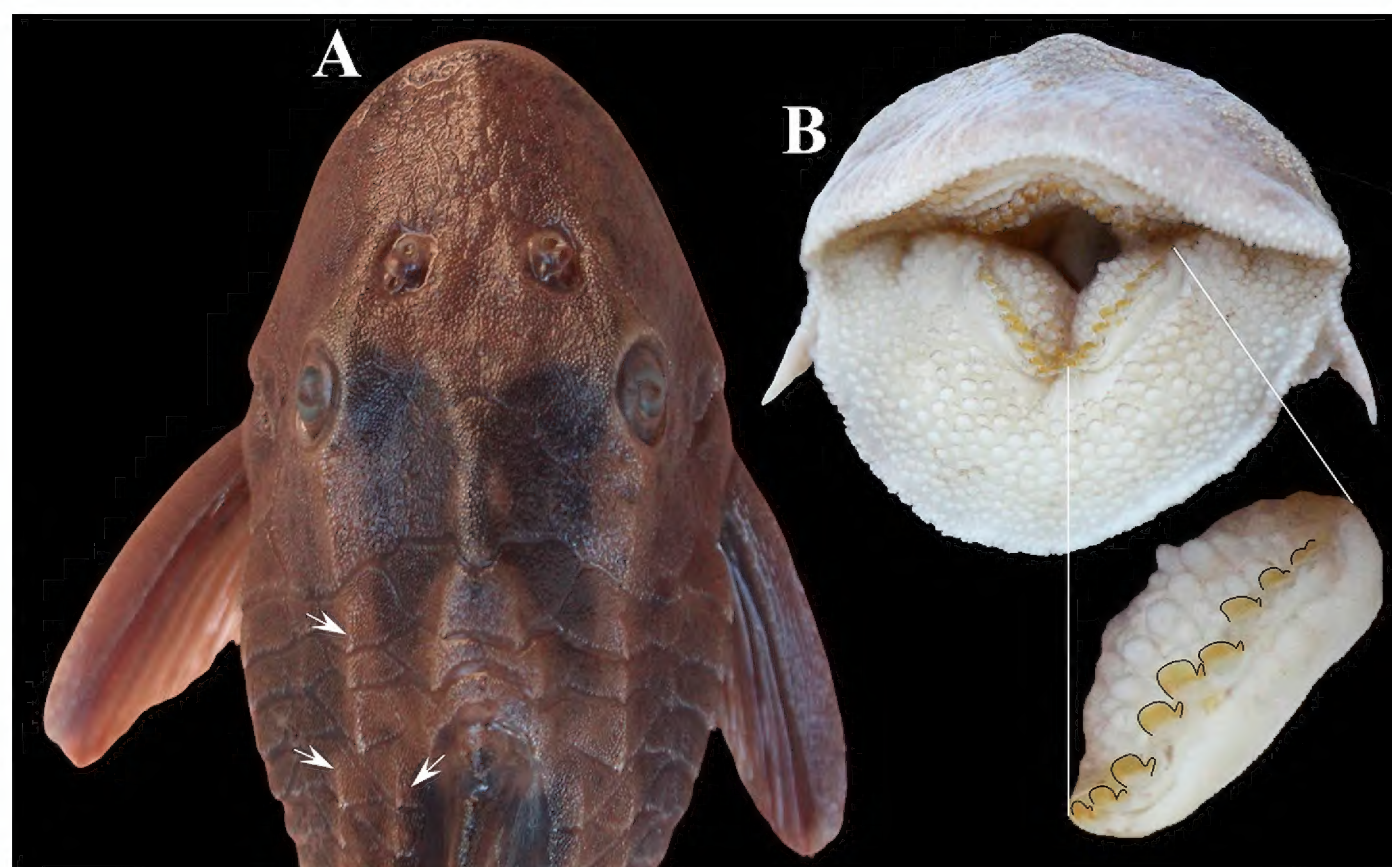


Figure 4. Additional diagnostic characters of *Hypostomus khimaera* collected in the upper rio Paraná basin (CITL 1015, 75.9 mm SL). **A.** Moderately developed keels (white arrows), with moderately developed odontodes (dorsal view). **B.** Mouth and teeth, with papillae not forming series in the inner face of upper and lower jaws, showing the detail of the teeth crowns (outlined in black).



rio Paraguay basin, this species occurs in syntopy with *H. cochliodon* and was historically identified as this species until Tencatt et al.'s (2014) revision of *H. cochliodon* in which they described *H. khimaera* and *H. basilisko*.

Explanations for the occurrence of *H. khimaera* in the upper rio Paraná basin follow two different lines: one is based on natural phenomena, and the other, on human activities. Natural phenomena that could account for ichthyofaunal exchange between the rio Paraguay and upper rio Paraná basins include temporary connections between the two basins during floods and past stream capture events. A series of geological faults existing in the upper rio Paraguay highlands theoretically make headwater captures possible (Ribeiro et al. 2011). Headwater captures have been reported between the upper rio Paraná and neighboring river basins, such as the São Francisco, Tocantins/Araguaia, and Paraguay, in addition to coastal river basins from southeastern Brazil (Aquino and Colli 2017; Dagosta and de Pinna 2019; Frota et al. 2019).

Additionally, in several places, headwater streams in the basins of the rios Aquidauana and Pardo are very close and may become temporarily connected during floods (a phenomenon known as “águas emendadas”, translated here as “headwaters connected by floods” in English) (Campestrini et al. 2014). Concurrently, the rio Paraguay and upper rio Paraná basins share several species due to natural causes, including *Oligosarcus pinto* Amaral-Campos, 1945, *Astyanax lineatus* (Perugia, 1891), and *Jupiaba acanthogaster* (Eigenmann, 1911); see Valério et al. (2007), Ferreira et al. (2017) and Lopes et al. (2023), and Lopes et al. (2020), respectively.

Alternatively, our new record of *H. khimaera* is from a tributary of the lower rio Anhanduí, which is more than 180 km away from the divide between the Pardo and Aquidauana river basins, and it is closer to the rio Paraná. This seems to weaken hypothesis that this occurrence is due to natural causes. Our second hypothesis to explain the origin of *H. khimaera* in the upper rio Paraná basin is that it is the result of a biological invasion in the Itaipu reservoir. The major invasion route into the upper rio Paraná basin is through the Itaipu Reservoir, whose filling in 1982 caused the permanent submersion of the Sete Quedas Falls, which suppressed the ancient biogeographic barrier separated the upper and lower basins of the rio Paraná. Even though this filling took place only once, the opening of the Canal da Piracema in 2002 provided a continuing pathway for fish dispersal between the two ecoregions (Júlio Junior et al. 2009). The Itaipu Reservoir and the Canal da Piracema together enabled a massive biological invasion event in the upper rio Paraná basin, which included the arrival *H. cochliodon* (Júlio Junior et al. 2009; Ota et al. 2018).

However, by suggesting that the presence of *H. khimaera* in the upper rio Paraná basin is the result of a biological invasion, we must make two important assumptions. First, we assume the species exists in the lower rio Paraná basin, and second, we assume that Nupélia researchers did not detect this species in the Itaipu Reservoir and on the upper rio Paraná floodplain despite decades of regular monitoring of fish in the region. The presence of *H. khimaera* in the lower rio Paraná basin has not been confirmed to date, even though there are no physical barriers between the Paraguay and lower Paraná river basins. The non-detection of this species in the lower rio Paraná basin may be a consequence of its absence in the ecoregion, sampling gaps, incorrect identifications, and/or possibly low abundance as a response to unknown ecological conditions.

Finally, there is the third possibility that the occurrence of *H. khimaera* in the upper rio Paraná basin is the result of intentional releases by humans, since *Hypostomus cochliodon* group species are appreciated by hobby aquarists (Novák et al. 2022). Other fish species are thought to have been introduced in the upper rio Paraná basin in this way (Garcia et al. 2018), which lends support to this hypothesis. However

plausible, with only a single specimen collected from an area that is distant from urban centers and with no evidence pointing to a specific person or group who might be responsible for introducing this species in the upper Paraná basin, this third hypothesis lacks support for now.

Finding the hypothesis that fits the data best will demand further fieldwork in the rio Pardo basin, sampling tissues for DNA analysis, and thoroughly reevaluating previously collected specimens. Specimens of *H. khimaera* from other localities in the ecoregion may be available in fish collections, perhaps misidentified as *H. cochliodon*, and their eventual discovery could reveal clues to the pathway through which *H. khimaera* has expanded its geographic range. Our first hypothesis would be corroborated by the discovery of additional specimens from the upper reaches of the rio Pardo basin and which share haplotypes with specimens from the rio Aquidauana basin. Our second hypothesis would be corroborated by the confirmation that *H. khimaera* is native to the lower rio Paraná basin, as well as by the finding of specimens collected in the Itaipu Reservoir or in the upper rio Paraná Floodplain within a time frame that makes possible the dispersion of this species to rio Pardo basin. If neither of the first two hypotheses finds support with new data, our third hypothesis will perhaps be the most likely.

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ADDITIONAL INFORMATION

Conflict of interest

The authors declare that no competing interests exist.

Ethical statement

No ethical statement is reported.

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Author contributions

Conceptualization: DAL and LFCT. Analysis of data: DAL and CHZ. Investigation: DAL, RNS, VCG, FRC, CHZ and LFCT. Project administration: DAL and RNS. Resources: DAL and RNS. Supervision: VCG, FRC, CHZ and LFCT. Writing – original text: DAL. Writing – review and editing: RNS, VCG, FRC, CHZ and LFCT.


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Data availability

All data that support the findings of this study are available in the main text.

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